

Intrinsic and extrinsic competitive interactions between two larval parasitoids of *Heliothis virescens*

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Abstract. 1. Competition between parasitoid species may be a key factor in the community dynamics of plant–herbivore–parasitoid systems and is an important consideration in the selection and management of effective biological control agents.

2. Interspecific competition can occur between adult parasitoids searching for hosts (extrinsic competition) and between multiple parasitoid larvae developing within a single host individual (intrinsic competition). A model system comprising the lepidopteran pest *Heliothis virescens* and two key hymenopteran endoparasitoids, *Microplitis croceipes* and *Cardiophiles nigriceps*, was employed to explore parasitoid host-location strategies and the consequences of intrinsic and extrinsic competitive interactions between parasitoid species.

3. The less specialised of the two parasitoids, *M. croceipes*, was found to have a shorter hatching time and to dominate intrinsic competition, except when its oviposition followed that of the more specialised parasitoid, *C. nigriceps*, by 16 h or more. This interval corresponded to the differential in hatching time between the two species.

4. *Cardiophiles nigriceps*, however, displayed superior host-searching efficiency that may compensate for its disadvantage in intrinsic competition. This parasitoid was more effective at detecting host infestation sites via airborne odours and at locating and attacking early instar host larvae than was *M. croceipes*.

Key words. *Cardiophiles nigriceps*, competition, *Heliothis virescens*, larval parasitoids, *Microplitis croceipes*, multiparasitism.

Introduction

Godfray (1994) reviewed the importance of competition as a factor influencing community structure. He stated ‘The true role of competition in parasitoid communities is most likely to be revealed by experimental studies of pairs and small groups of species’. In addition to being of ecological importance, understanding the dynamics of competitive interactions between parasitoid species is relevant to the selection of effective biological control agents for importation and release (Mackauer, 1990), to the development of habitat management

and cultural practices to conserve and enhance the abundance and efficacy of beneficial species (Hawkins, 1993), and to efforts to predict the outcome of such endeavours (Murdoch & Briggs, 1996). Thus, understanding the competitive interactions between biological control agents enhances the ability to understand and predict the interactions of natural enemy populations with their host.

Competition between natural enemy species influences the size, structure, and stability of insect communities (Force, 1974, 1985; Price *et al.*, 1988). Because the availability of hosts is critical for parasitoid reproduction (Bolter & Laing, 1983; Hawkins, 1988; Mackauer, 1990), local host scarcity may lead to intense inter- and intra-specific competition (Hågvar, 1989; van Alebeek *et al.*, 1993). This is particularly true for solitary endoparasitoid species in which only one individual can develop to maturity within a single host (Vinson

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& Iwantsch, 1980). Competitive interactions at the level of host location by adult parasitoids are referred to as extrinsic competition. In contrast, intrinsic competition comprises competitive interactions between multiple parasitoid larvae developing within a single host individual (Godfray, 1994).

The outcome of extrinsic competition among parasitoids may be influenced by differences in the parasitoids' host-finding efficiency, reproductive capacity, and phenological synchronisation with the host (Hågvar, 1989; Lewis *et al.*, 1990; Tumlinson *et al.*, 1993). Once parasitised, hosts are often rendered unsuitable for exploitation by a second parasitoid (Hågvar, 1989). Thus, females with highly effective host location strategies may have a competitive advantage that becomes particularly important when local host density is low (Godfray, 1994). When multiple parasitism does occur, the outcome of intrinsic competition is affected by differences in parasitoid development rates, egg number, the developmental stage of the host, the order in which oviposition occurs, and the time interval between the first and second oviposition (van Strien-van Liempt, 1983; Tillman & Powell, 1992). Parasitoid reproductive success depends in part, therefore, on mechanisms that deter subsequent ovipositions or eliminate super-numerary parasitoids (Jervis & Kidd, 1996).

Conflict between parasitoid larvae developing within a host individual may be divided into two basic categories: physical attack and physiological (e.g. chemical) suppression (Clausen, 1940; Fisher, 1961; Salt, 1961; Bartlett & Ball, 1964; Stary, 1970; Vinson, 1972; Vinson & Iwantsch, 1980). First-instar larvae of many solitary hymenopteran parasitoids are equipped with large mandibles (Fisher, 1961; Salt, 1961). Fighting often occurs between larvae of similar age, although first-instar larvae of some species attack and kill later-instar larvae that lack or have reduced mandibles (Chow & Mackauer, 1984, 1985, 1986). Nevertheless, possession of large mandibles by first-instar larvae does not guarantee that physical attack is the mechanism employed to eliminate rivals (Strand, 1986; Mackauer, 1990). Physiological suppression is also common and may occur by toxic secretion shortly after eclosion of the embryo, by starvation or asphyxiation of competitors later in larval development, or as a result of toxins or viruses injected by the adult female during oviposition (Mackauer, 1990).

The study reported here addressed competitive interactions between *Cardiochiles nigriceps* and *Microplitis croceipes*, two key endoparasitoids of the tobacco budworm *Heliothis virescens* (Lepidoptera: Noctuidae), a major pest of cotton and tobacco. Both of these braconid wasps attack larval stages of their hosts. They overlap in much of their geographical range and many of their habitat requirements. *Microplitis croceipes* is host-specific within the *Heliothis/Helicoverpa* complex on a wide variety of cultivated and uncultivated plants (Stadelbacher *et al.*, 1984), whereas *C. nigriceps* is a highly specialised parasitoid that utilises *H. virescens* almost exclusively (Chamberlin & Tenhet, 1926; Vinson & Iwantsch, 1980). Although once numerous (King *et al.*, 1985), *M. croceipes* has undergone a rapid population decline in recent years and has almost disappeared from cotton fields in Georgia. This study was designed to explore the strategies by which these parasitoids locate and utilise their common host

and the consequences of their intrinsic and extrinsic competitive interactions in order to improve understanding of the dynamics of plant-herbivore-parasitoid systems.

Material and methods

Study organisms: background information

Microplitis croceipes. *Microplitis croceipes* is distributed widely within the United States from New Jersey to Georgia, west to New Mexico, Arizona, Utah and Oregon (Krombein *et al.*, 1979). It is an important parasitoid of *Heliothis virescens* and *Helicoverpa zea* (Quaintance & Brues, 1905; Neunzig, 1963; Lewis & Brazzel, 1966, 1968; Snow *et al.*, 1967; Bottrell *et al.*, 1968; Lewis & Snow, 1971; Young & Price, 1975; Smith *et al.*, 1976; Marsh, 1978; Stadelbacher *et al.*, 1984; King *et al.*, 1985; Tillman & Powell, 1996). Although *M. croceipes* can attack and develop in all but the late fifth instar of *Heliothis* and *Helicoverpa* (Lewis, 1970), it exhibits a preference for third-instar larvae (Lewis, 1970; Hopper & King, 1984). Development time is influenced by host instar but not by host species, and the wasp shows no preference between similar-aged caterpillars of the two hosts (Hopper & King, 1984).

Microplitis croceipes attacks *Heliothis* and *Helicoverpa* on a wide variety of cultivated crops such as alfalfa, corn, cotton, potato, sesame, sorghum, soybean, tobacco and tomato (Butler, 1958; Neunzig, 1963; Lewis & Brazzel, 1966; Young & Price, 1975; Smith *et al.*, 1976; Pair *et al.*, 1982; Stadelbacher *et al.*, 1984; King *et al.*, 1985; Puterka *et al.*, 1985; Manley *et al.*, 1991). *Microplitis croceipes* has also been reported to attack *H. virescens* and *H. zea* in non-cultivated host plants such as crimson clover, cranesbill, ground cherry, peppergrass, johnsongrass and smartweed (Lewis & Brazzel, 1966; Roach, 1975; Smith *et al.*, 1976; Mueller & Phillips, 1983; Stadelbacher *et al.*, 1984; Rathman & Watson, 1985). *Microplitis croceipes* is believed to offer great potential as a biological control agent against *Heliothis/Helicoverpa* species (Burris *et al.*, 1995), although in some parts of its range, such as Georgia where this parasitoid was once abundant, it has almost disappeared (J. R. Ruberson, pers. comm.).

Cardiochiles nigriceps. *Cardiochiles nigriceps* is a solitary larval endoparasitoid that principally attacks *H. virescens* (the tobacco budworm), and is an important factor in the natural control of this pest on tobacco, the caterpillar's main food plant, and also on cotton in the south-eastern U.S.A. (Lopez, 1982). It is found from the District of Columbia to Florida and west to Kansas and Louisiana (Marsh, 1978), and is also found in Colombia, South America. *Cardiochiles nigriceps* generally lays a single egg in a host larva and all host instars may be used (Vinson, 1972). The parasitoid larva has three instars and usually remains as a prepupal stage until the host larva is fully mature and enters the soil to pupate (Lewis & Vinson, 1968; Danks *et al.*, 1979). In the southern U.S.A., *C. nigriceps* completes several generations a year, and most of the autumn generation overwinters in the soil as diapausing prepupae (Danks *et al.*, 1979). *Cardiochiles nigriceps* has been

recovered from hosts collected in tobacco, spider flower, ground cherry, toadflax, deergrass, Florida beggarweed and cotton (Neunzig, 1963; Snow *et al.*, 1967). In the southern U.S.A., where the parasitoid and its host occur together naturally, *C. nigriceps* provides significant natural control of *H. virescens*.

Heliothis virescens. The tobacco budworm *H. virescens* (Fabricius) is distributed world-wide (King & Jackson, 1989). In the U.S.A., it is most injurious to crops in the Gulf states (Metcalf & Metcalf, 1993). Annual economic losses to *Heliothis* worldwide are estimated in billions of dollars. In the U.S.A. alone, *H. zea* and *H. virescens* cause damage of about \$1.25 billion annually (Jackson *et al.*, 1989; Burris *et al.*, 1995). *Heliothis virescens* eggs are deposited on food plants used by the larvae, which are typically tobacco and cotton, but also ground cherry, tomatoes, other solanaceous plants, geranium and ageratum (Metcalf & Metcalf, 1993). During the course of the summer in the south-eastern United States, there are three to six generations, while to the north the number decreases to two or three in the central states, and probably a single generation in Canada. The tobacco budworm passes the winter as a pupa beneath the surface of the soil, emerging as a moth early in the spring.

Each female may lay from 500 to 3000 eggs, which are deposited singly over the plants; in cotton, most frequently in the buds and squares (King & Jackson, 1989). Eggs hatch after 2 or 3 days during the warmer parts of the summer and the larvae begin feeding. The larvae moult five or six times and complete development in about 2 weeks in hot weather, after which they leave the food plant and burrow into the soil to pupate. The pupal stage lasts for 2 weeks before the adults of the next generation emerge. After the latter have been out for several days, egg laying begins. In the middle of the summer in the Cotton Belt of the U.S.A., the entire life-cycle occupies only 30–35 days, while in the spring and autumn, and in more northern localities, it may extend over 2 months (Metcalf & Metcalf, 1993).

Study organisms: rearing information

Parasitoids. *Microplitis croceipes* and *C. nigriceps* were reared on *H. virescens* larvae according to the procedure of Lewis and Burton (1970). Both species were held at 25 °C, LD 14:10 h, and 70% RH. All experiments were conducted with mated *M. croceipes* and *C. nigriceps* females, 2- and 5-days-old, respectively.

Hosts. Larvae of *H. virescens* were obtained from USDA-ARS Gainesville, Florida. Larvae of *H. zea* were obtained from the Insect Biology and Population Management Research Laboratory (IBPMRL), USDA-ARS, Tifton, Georgia. Larvae were fed a laboratory-prepared pinto bean diet (Perkins *et al.*, 1973) and held in a climatic room at 25 °C, LD 14:10 h, and 70% RH until used for experiments.

Plants. Tobacco plants (*Nicotiana tabacum*, K 326 variety) were grown in a glasshouse at 25:30 °C, LD 15:9 h, 60 ± 20% RH from seeds planted in a 1:1 mixture of

peatmoss (Promix Bx®) and potting soil fertilised with Osmocote®. Seven- to 9-week-old plants were used in the experiments.

Biossay procedures

Intrinsic competition. Three types of experiment were conducted to assess intrinsic competitive interactions between larvae of the two parasitoid species.

(1) Survival and successful development: an individual second-instar *H. virescens* larva was exposed to a mated female of one parasitoid species in a Petri dish and observed until a single oviposition occurred. After a specific time interval, the once-parasitised larva was exposed to a mated female of the second parasitoid species. The variables manipulated were order of parasitism (i.e. which species oviposited first) and time interval between ovipositions (0, 1, 4, 8, 16, 24, and 48 h). Three replicates of 30 trials each were performed for each order of parasitism at each of the seven time intervals (total 1260 trials). Following each trial, the parasitised larva was reared on artificial diet in an individual container until a parasitoid cocoon developed. The frequency of emergence was recorded for each parasitoid species, along with the mortality of host larvae that failed to produce parasitoids.

(2) Physical vs. physiological suppression: a similar design was employed to determine whether competition by parasitoid larvae was expressed through physical attack or through physiological suppression. Multiply parasitised host larvae were obtained through the procedure described above. Dissections of larvae were then carried out at specified time intervals (0, 8, 16, and 24 h) following the second oviposition. Each host larva was placed in a drop of Ringer solution in a wax tray and opened under a dissecting microscope. Twenty dissections were made at each time interval for each order of oviposition (i.e. *M. croceipes*/*C. nigriceps*, *C. nigriceps*/*M. croceipes*).

(3) Hatching time: to investigate the possible effect of relative hatching times on the outcome of parasitoid larval competition, 60 third-instar host larvae, each parasitised by a single parasitoid species (120 total), were dissected at various times between 24 h and 62 h following oviposition (several larvae each half hour) in order to determine the time interval between oviposition and hatching. Dissections followed the procedure described above.

Extrinsic competition. Two types of experiment were conducted to examine how the two parasitoid species compare in their ability to locate and successfully parasitise host larvae.

(4) Long-range detection: two tobacco plant terminals, one damaged by two first-instar *H. virescens* larvae and one without any caterpillar damage, were removed from the plant stem. Each terminal, consisting of the three youngest leaves, was wrapped in wet cotton and aluminium foil (to minimise green leaf volatiles emanating from the wound) and placed in a 125-ml Erlenmeyer at the upwind end of the wind tunnel. A female parasitoid was released at the downwind end. The first

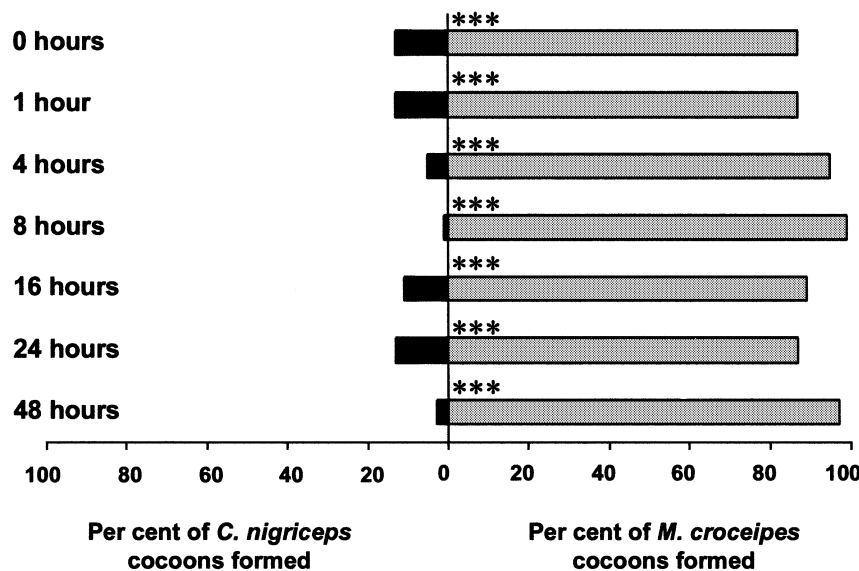


Fig. 1. Percentage emergence by *C. nigriceps* and *M. croceipes* when *M. croceipes* was the first to oviposit. Hours indicate the time between first and second oviposition. Asterisks indicate significant difference within each time interval (*t*-test, *** $P < 0.001$).

plant terminal (damaged or undamaged) on which the female landed was recorded. Females of each species were tested alternately. Ten complete flights of each species were conducted and three replications of 10 flights each were performed on different days. The positions of the plants were switched after five flights by each species to correct for potential side preference in the parasitoids.

Wind tunnel. Experiments were conducted in a $50 \times 50 \times 120$ cm wind tunnel (Drost *et al.*, 1986) at a wind speed of $45 \pm 2 \text{ cm s}^{-1}$ (*M. croceipes*) and $60 \pm 2 \text{ cm s}^{-1}$ (*C. nigriceps*) at $25 \pm 2^\circ\text{C}$ and $40 \pm 10\%$ RH. Different wind speeds were used to obtain maximum performance of flights for each parasitoid species.

(5) Short-range detection: a tobacco leaf was placed in a 150×30 mm Petri dish with five tobacco budworm larvae. A female parasitoid was introduced and allowed to oviposit freely for 5 min and the number of larvae parasitised was recorded. Females of each species were tested alternately. The leaf was replaced after both species completed four trials. First, second and third instars of *H. virescens* were tested. For each instar, 24 replications were performed with each parasitoid species (144 total trials).

(6) First-instar host detection: twelve laboratory-reared, first-instar caterpillars were placed on the leaves (two caterpillars/leaf) of 8-week-old, potted, glasshouse-grown tobacco plants 24 h prior to placement in the field. Six tobacco plants were placed in a cotton field with an active population of *C. nigriceps*. The plants were arranged 80 cm apart in a 3×2 design. The number of larvae parasitised in a period of 2 h was observed and recorded. Each bioassay was conducted on 3 days to account for day-to-day variation. This experiment was not conducted with *M. croceipes* because of the scarcity of this parasitoid in the field.

Data analysis

Analysis of variance (GLM procedure, SAS Institute, 1988) was used for data analysis of experiments 1 and 5. A *t*-test was performed to identify significant differences within each time interval between the two parasitoids (expt 1). Results of all dual-choice tests (expt 4) were analysed with chi-squared tests, to which the Yates correction for continuity was applied. All tests were performed with $P < 0.05$.

Results

Intrinsic competition

Survival and successful development (expt 1). Survival and dominance by competing parasitoids within the same host species were dependent on both order of parasitism ($F = 412.99$, $P < 0.001$) and time interval between primary and secondary oviposition ($F = 39.96$, $P < 0.001$). The interaction between these two factors ($F = 39.43$, $P < 0.001$) also produced highly significant effects. Examination of multiple parasitism revealed that *M. croceipes* larvae were dominant in most cases. When both parasitoids oviposited at approximately the same time, a *M. croceipes* larva eventually emerged in 87% of the trials (Figs 1 and 2). When *M. croceipes* oviposited first, larvae of this species were dominant approximately 90% of the time, without regard to the time interval between primary and secondary oviposition (Fig. 1). *Microplitis croceipes* was also dominant when *C. nigriceps* oviposited first, as long as the interval between primary and secondary oviposition did not exceed 8 h. In cases where *C. nigriceps* oviposition preceded *M. croceipes* oviposition by 16 h or more, *C. nigriceps* larvae were dominant (Fig. 2).

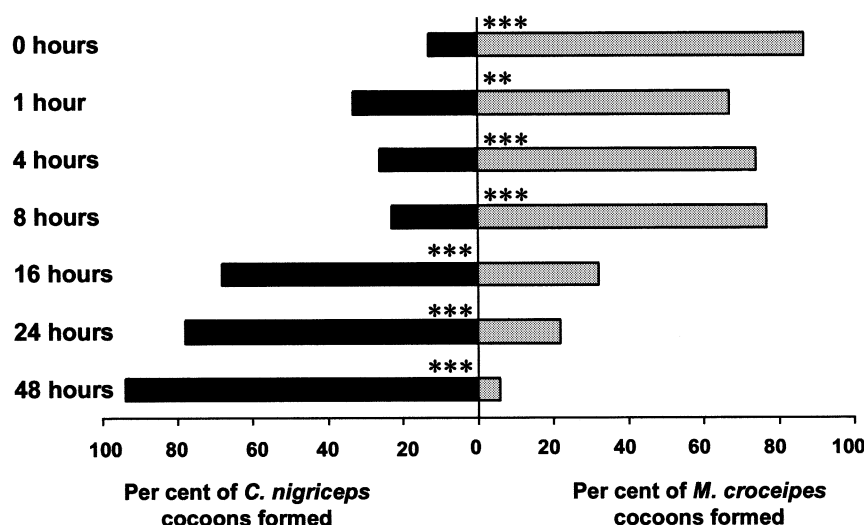


Fig. 2. Percentage emergence by *C. nigriceps* and *M. croceipes* when *C. nigriceps* was the first to oviposit. Hours indicate the time between first and second oviposition. Asterisks indicate significant difference within each time interval (*t*-test, ** $P < 0.01$, *** $P < 0.001$).

Physical vs. physiological suppression (expt 2). Dissections revealed that the eggs of both species hatched in all cases. When oviposition by *M. croceipes* preceded that of *C. nigriceps* or followed it by less than 16 h, *C. nigriceps* larvae were small, with head capsules that failed to tan and were encapsulated. When *M. croceipes* oviposition followed *C. nigriceps* by 16 h or more, the outcome was reversed and *M. croceipes* larvae exhibited incomplete development. In either case, the larvae showed no evidence of physical injury, indicating that larval competition is expressed through physiological suppression (although the mechanism of suppression is not yet known). Suppressed larvae failed to grow and were inactive, but were still alive at the time of dissection.

Hatching time (expt 3). Dissections showed that *M. croceipes* eggs hatched 36–39 h following oviposition, whereas *C. nigriceps* eggs required 48–52 h to hatch.

Extrinsic competition

Long-range detection (expt 4). *Cardiochiles nigriceps* exhibited significant preference for the damaged leaf terminal over the undamaged leaf terminal ($\chi^2 = 6.45$, $P < 0.05$), whereas *M. croceipes* displayed no significant preference ($\chi^2 = 0.3$, $P = \text{NS}$; Fig. 3).

Close range detection (expt 5). *Cardiochiles nigriceps* was significantly more efficient than *M. croceipes* in locating first- ($T = 10.85$, $P < 0.001$), second- ($T = 10.40$, $P < 0.001$), and third- ($T = 0.35$, $P < 0.001$) instar larvae. *Cardiochiles nigriceps* located an average of 50% of first-instar larvae and 100% of second- and third-instar larvae within 5 min, whereas *M. croceipes* was incapable of locating first-instar larvae and only located an average of 46% of second-instar larvae and 70% of third-instar larvae (Fig. 4).

First-instar host detection (expt 6). When the first-instar larvae were placed in the tobacco plants in the cotton field for 2 h, 80% of the larvae placed in the plants were stung, indicating that in a natural environment *C. nigriceps* is able to locate and parasitise first-instar larvae effectively.

Discussion

The short hatching time and rapid growth rate of *M. croceipes* larvae appear to explain much of the dominance of this species in intrinsic competition. The 16-h developmental head-start required for *C. nigriceps* to become dominant corresponds closely with the observed difference in embryonic development between the two parasitoids. In each case, only the dominant larva survived to emergence, while the larva of the other species was suppressed.

Suppressed larvae failed to develop but showed no evidence of physical injury. The possibility of physical attack cannot be discounted, however, because young instars of both parasitoids have large mandibles and cases of physical attack have been documented for both *C. nigriceps* (Vinson & Iwantsch, 1980) and *M. croceipes* (Tillman & Powell, 1992). Nevertheless, previous work has shown that, in most cases, deceased parasitoid larvae lacking any evidence of physical attack are indicative of physiological suppression (Mackauer, 1990). These observations were therefore interpreted as evidence that intrinsic competition between these two species is expressed through physiological suppression (by an as-yet-unknown mechanism).

Cardiochiles nigriceps was found to be the dominant species in extrinsic competition, displaying superior host-location efficiency involving both long-range (volatile) and short-range (contact) cues (both of which are known to be important in the host selection sequence; Vet *et al.*, 1995), and an ability to

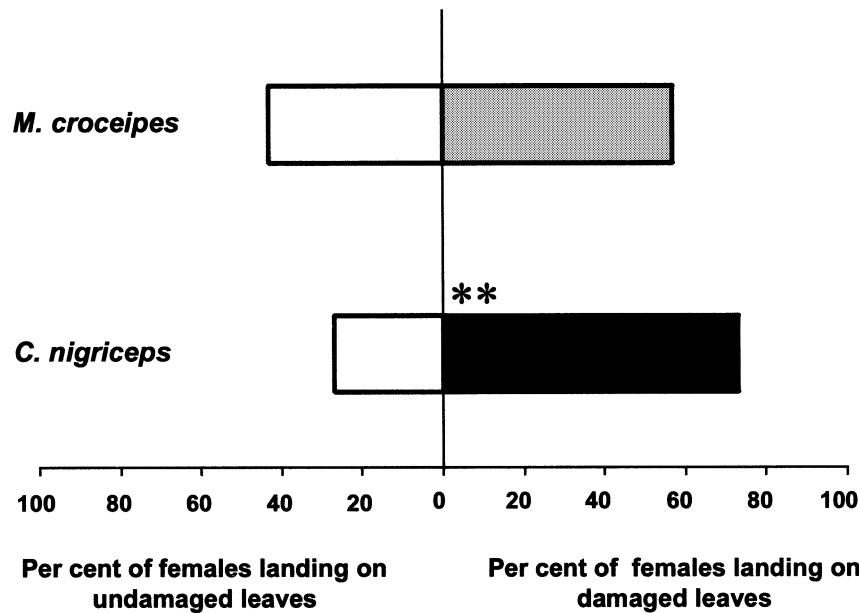


Fig. 3. Flight response by *C. nigriceps* and *M. croceipes* to undamaged and larval-damaged tobacco leaves in dual-choice tests. Bars indicate percentage of female choice for each odour source. Asterisks indicate significant differences (chi-squared, $**P < 0.01$).

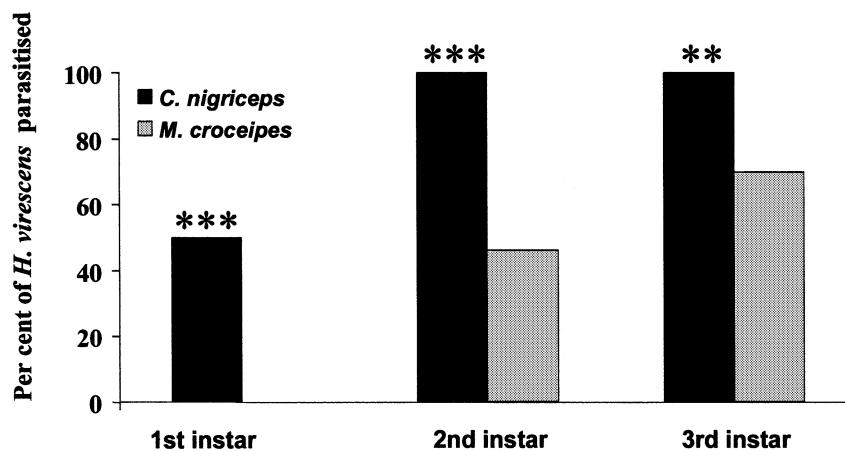


Fig. 4. Percentage of *H. virescens* larvae in three different instars parasitised by *C. nigriceps* and *M. croceipes* females. Asterisks indicate significant difference (ANOVA, $**P < 0.01$, $***P < 0.001$).

exploit early-instar hosts that are not utilised by *M. croceipes*. Because the first instar of *H. virescens* lasts for 2 days or longer, the ability of *C. nigriceps* to exploit this instar may more than compensate for the intrinsic competitive advantages of *M. croceipes*. Field studies by Tillman and Powell (1996) comparing the efficiency of these two parasitoid species showed that a higher level of host parasitisation was accomplished by *C. nigriceps* in both low and high host densities, leading them to conclude that *C. nigriceps* should outperform *M. croceipes* in a cotton field. Furthermore, *C. nigriceps* is able to distinguish between host and non-host

infestations on phylogenetically distant plant species (tobacco and cotton) by exploiting herbivore-specific volatile emissions (De Moraes *et al.*, 1998). Although a specialist, *M. croceipes* apparently has only a poor ability to distinguish host infestations from non-host before alighting on a plant, and decisive host recognition may require non-volatile chemicals in the frass (McCall *et al.*, 1993; Cortesero *et al.*, 1997).

The dominance of *Cardiochiles nigriceps* in locating host individuals may be related to the highly specialised nature (narrow host range) of this parasitoid. Specialised adaptations, such as an ability to locate hosts successfully at early instars and

in low densities, as shown by Tillman and Powell (1996), can compensate for losses suffered in intrinsic competition. Such adaptations, through which relatively poor intrinsic competitors acquire superior dispersal or host-finding ability, have been termed evasive strategies (Zwölfer, 1979) and are reported in many guilds of phytophagous and parasitic insects (Zwölfer, 1979; Pschorn-Walcher, 1987). Zwölfer (1971) termed the case in which one competitor has an advantage in the intrinsic competition and the other is extrinsically superior counter-balanced competition. Zwölfer (1971), Schröder (1974) and colleagues have argued that the coexistence of parasitoids on a number of forest pests can be explained by counter-balanced competition and have classified the parasitoids of these insects as either intrinsically or extrinsically superior competitors.

Microplitis croceipes and *C. nigriceps* have similar requirements with regard to hosts and habitats. Both are solitary larval endoparasitoids of *H. virescens*. *Microplitis croceipes* also parasitises *H. zea*, but wind tunnel experiments have shown that cotton plants damaged by *H. virescens* are more attractive to this parasitoid than are those damaged by *H. zea* (C. M. De Moraes, unpublished). Thus, they may be expected to compete intensively for host resources. It is conceivable that counter-balanced competition may have played a role in the historical coexistence of *M. croceipes* and *C. nigriceps*. If so, a disruption of this competitive balance may be responsible for the recent decline of *M. croceipes* in the field. One possibility is that the high use of pesticides during boll weevil eradication has affected *M. croceipes* adversely and acutely; this parasitoid appears to be more susceptible to pesticides than is *C. nigriceps* (Tillman & Powell, 1995). *Microplitis croceipes* has also experienced decline in regions that have not experienced boll weevil eradication, however, suggesting that other causes may also be involved. Although such speculation may have heuristic value, a great deal of additional information would be required to make any definitive statements about the role of competitive displacement in the decline of *M. croceipes*. Further research will be needed to assess the interrelationships between parasitoid competitive interactions, human agricultural practices (including relative pesticide susceptibility; Tillman & Powell, 1992, 1995), and other potentially interacting ecological factors and their relative importance in determining the community structure and dynamics in this and other plant-herbivore-parasitoid systems.

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